

# Extinctions in large ecosystems under periodic and chaotic forcing

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We consider a model for plankton ecosystems with resources, self-limitation effects, and time dependent parameters. The model takes into account the extinction of multiple species. We show that the model is well posed and investigate its dynamical properties. The number of species which can coexist depends on both parameters and forcing. Our numerical simulations show that the system is more stable under chaotic forcing.

**Phytoplankton are a critical component of Earth's carbon cycle and thus play an important role in the climate system. They are sensitive indicators of climate change. As a key part of the global ecosystem, they influence climate feedback processes and possible tipping points. The complex plankton ecosystem has been studied in terms of internal processes within the ecosystem such as the competition for resources, conditions for chemical reactions, etc. However, recent observations have shown that climate change can be a leading factor influencing ecosystem behavior.**

**Here we suggest a mathematical model of a plankton ecosystem with many species, which exhibits complicated behavior under time periodic or chaotic parameter oscillations. These oscillations can model the influence of environmental temperature oscillations. A new element of this model, with respect to previous ones, is that we take into account species extinctions.**

## I. INTRODUCTION

Models of large ecosystems form an important class of dynamical systems generating complicated patterns and strange (chaotic) attractors. However, modeling these large systems is made difficult by rapid, small scale biological evolution and gaps in observations to use for comparison. Also, there is uncertainty in how to set up reliable experiments on such ecosystems.

A well studied example is the ocean ecosystem, where the main resource for many species is phytoplankton. Phytoplankton plays an important role in the dynamics of the climate system through the oceanic carbon cycle by removing about half of all carbon dioxide from the atmosphere during photosynthesis<sup>1</sup>. Previous studies<sup>2,3</sup> have shown that phytoplankton communities respond to climate warming through changes in diversity and productivity. However, it was determined<sup>4</sup> that changing the climate temperature directly impacts

the chemical cycles in plankton, affecting the system as much as nutrients and light.

Another example where environmental temperature may be related to the dynamics of the plankton ecosystem is the very recent appearance of a *fall* phytoplankton bloom in the Arctic Ocean<sup>5</sup>. In contrast to previous observations, the new plankton dynamics may be approaching a possible bistable regime, where plankton bloom not only during the spring time, but in early fall as well. This in turn could affect surface ocean temperature and delay sea ice re-freezing. Also, an unusual massive phytoplankton bloom which has been found *underneath* the Arctic ice pack in the Chukchi Sea<sup>6</sup> may correlate with planetary warming. Thus, theoretical investigation of the dynamical properties of large ecosystems under external forcing makes a significant contribution to understanding properties of the ecosystems as well as the climate system.

We consider here a new phytoplankton model, which takes into account resources, self-limitation effects, and species extinctions. The model parameters depend on the state of the environment via time dependent coefficients. This system is connected with some phytoplankton models, and under certain assumptions can be derived from them. If the resource turnover rate is large enough, the model reduces to a Lotka-Volterra system<sup>7</sup>. If we remove self-limitation effects for the Lotka-Volterra system, one finds<sup>8,9</sup> that a single species can survive only in an ecosystem for certain fixed climate parameters. Biologically, it is the exclusion principle. In the framework of the phytoplankton model, it is the so-called *plankton paradox* studied in many interesting works<sup>10-13</sup>. In fact, in contrast to the exclusion principle, we observe the coexistence of many plankton species sharing the same niche. Numerical simulations<sup>10-12</sup> have shown that in such systems chaos and unpredictable behavior occur. In the papers<sup>14,15</sup> it was shown that a temporal variability of the nutrient supply can lead to coexistence of species.

In this paper, we extend the model of Huisman and Weissing<sup>12</sup> by introducing self-limitation for species and species extinctions. Such an extended model can describe the coexistence of many species when self-regulation is stronger than species competition.

Our primary goal is to compare the two following situations: A) system with fixed parameters; B) the same system

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with time dependent parameters. In case B we consider two situations: time periodic oscillations and time chaotic ones.

The paper is organized as follows. In the next section we state the standard model of species coexistence. Further, we prove a general assertion on attractor existence for this model. For the case of a single resource we show that the global attractor consists of equilibria and derive an equation for species abundances. For large turnover  $D$  this equation has a simple asymptotic solution.

In Section III we introduce the new extended model, which takes into account species extinctions and time oscillations of the resource  $S$ . We also prove the existence of a compact global attractor when  $S = \text{const}$ . For the model with time dependent parameters we describe two situations where we can find asymptotic solutions. In Section IV we describe the results of numerical simulations.

## II. THE STANDARD MODEL OF PLANKTON BIODIVERSITY

We consider the following standard model of plankton biodiversity<sup>12</sup>:

$$\frac{dx_i}{dt} = x_i(-r_i + \rho_i(v) - \sum_{j=1}^N \gamma_{ij} x_j), \quad (1)$$

$$\frac{dv}{dt} = D(S - v) - \sum_{j=1}^N c_j x_j \rho_j(v), \quad (2)$$

where

$$\rho_j(v) = \frac{a_j v}{K_j + v}, \quad a_j, K_j > 0, \quad (3)$$

are Michaelis-Menten's functions,  $x_i$  are species abundances,  $r_i$  are the species mortalities,  $D$  is the resource turnover rate,  $S$  is the supply of resource  $v$ , and  $c_i$  is the content of the resource in the  $i$ -th species. These constants define how different species share resources. Note that if  $c_i = 0$  then the equation for  $v$  becomes trivial and  $v(t) \rightarrow S$  for large times  $t$ , i.e., the resource equals the resource supply.

The terms  $\gamma_{ii}x_i$  define self-regulation of species populations that restrict the species abundances, and  $\gamma_{ij}x_j$  with  $i \neq j$  define a possible competition between species for resources.

The coefficients  $a_i$  are specific growth rates and the  $K_i$  are self-saturation constants. The coefficients  $c_i$  determine how the species share the resource (nutrient supply). It is natural thus to assume that  $\sum_{i=1}^N c_i = 1$ ,  $c_i > 0$ .

When  $\gamma_{ij} = 0$  this system is equivalent to those in works where the plankton paradox<sup>12</sup> is studied (see the previous section). For the case of  $M$  resources we have more complicated equations

$$\frac{dx_i}{dt} = x_i(-r_i + \phi_i(v) - \sum_{j=1}^N \gamma_{ij} x_j), \quad (4)$$

$$\frac{dv_j}{dt} = D_j(S_j - v_j) - \sum_{k=1}^N c_{jk} x_k \phi_k(v), \quad (5)$$

where  $v = (v_1, v_2, \dots, v_M)$ , and

$$\phi_j(v) = \min\left\{\frac{a_j v_1}{K_{1j} + v_1}, \dots, \frac{a_j v_M}{K_{Mj} + v_M}\right\}. \quad (6)$$

where  $a_j$  and  $K_{ij} > 0$ . This model is widely used for primary producers like phytoplankton and it can also be applied to describe competition for terrestrial plants<sup>11</sup>. Relation (6) corresponds to the von Liebig minimum law, but we can consider even more general  $\phi_j$  satisfying the conditions

$$\phi_j(v) \in C^1, \quad 0 \leq \phi_j(v) \leq C_+, \quad (7)$$

where  $C_+ > 0$  is a positive constant, and

$$\phi_k(v) = 0, \quad \forall k \quad v \in \partial \mathbf{R}_+^N \quad (8)$$

where  $\partial \mathbf{R}_+^N$  denotes the boundary of the positive cone  $\mathbf{R}_+^N = \{v : v_j \geq 0, \forall j\}$ . Note that condition (8) holds if  $\phi_j$  are defined by (6). Similarly as above, we assume that  $\sum_{k=1}^N c_{ik} = 1$ ,  $c_{ik} > 0$ .

### A. General properties of the standard model

Let us first describe some sufficient conditions which guarantee that systems (1), (2) and (4), (5) are dissipative and have a global attractor. Define the matrix  $\Gamma$  with the entries  $\gamma_{ij}$  to satisfy the following condition (this is a classical assumption<sup>9</sup>):

**Assumption.** The matrix  $\Gamma$  with the entries  $\gamma_{ij}$  has a positive dominant diagonal:

$$\gamma_{ii} - \sum_{j \neq i} |\gamma_{ij}| = \kappa_i > 0. \quad (9)$$

This assumption means that species self-regulation is stronger than competition between species. Then, we can assert that the solutions to (4), (5) are non-negative and bounded.

**Lemma II.1.** Assume the  $\phi_j$  satisfy (7). Let us consider for (4), (5) the Cauchy problem with positive initial data for  $x$  and bounded positive initial resources

$$x_i(0) > 0, \quad v_j(0) \in (0, S_j). \quad (10)$$

Then solutions of this Cauchy problem are positive and a priori bounded, that is,

$$0 < v_j(t) < S_j, \quad 0 < x_i(t) < M_i, \quad t > 0, \quad (11)$$

where the  $M_i$  are positive constants.

**Proof.** The proof is standard. Let us prove that  $v_j(t) > 0$ . Assume that this fact is violated. Then there exists an index  $j_0$  and a time  $t_0 > 0$  such that

$$v_{j_0}(t_0) = 0, \quad \frac{dv_{j_0}}{dt} \leq 0, \quad v_j(t_0) \geq 0, \quad \text{for all } j \neq i. \quad (12)$$

Condition (8) entails that the term  $\sum_{k=1}^N c_{jk} x_k \phi_k(v)$  equals zero. Then we substitute these inequalities into the  $j_0$ -th equation (5) and obtain a contradiction.

In a similar way, we can prove that  $v_j(t) < S_j$ . Here, we use the positivity of the  $c_{jk}$  and  $\phi_k$  which implies

$$\frac{dv_j}{dt} \leq D_j(S_j - v_j).$$

Positivity of  $x_i$  follows from the fact that the  $i$ -th right hand side of system (4) is proportional to  $x_i$ , thus,  $x_i(t) = x_i(0) \exp(\xi_i(t))$ , where  $\xi_i$  is a function.

Let us prove that  $x_i(t) < M_0$  for some  $M_0 > 0$ . Let  $E(t) = \max\{x_1(t), \dots, x_N(t)\}$ . Let us estimate  $dE/dt$  for large  $E$ . Let  $i_0(t)$  be an index such that  $E(t) = x_{i_0}(t)$ . According to (7) the  $\phi_i$  are uniformly bounded by  $C_+$ . Therefore within any open interval, where  $i_0$  is fixed, one has

$$\frac{dx_{i_0}}{dt} \leq x_{i_0} R_{i_0}, \quad R_{i_0} \leq C_+ - \kappa_i x_{i_0}(t),$$

where  $\kappa_i > 0$  due to assumption (9) on  $\Gamma$ . Thus, if  $E$  is large enough,  $R_{i_0}$  is a negative number and  $\frac{dx_{i_0}}{dt} < 0$ . Thus  $E$  is bounded, which completes the proof.

We then obtain the following corollary.

**Lemma II.2.** *Under the conditions of the previous lemma, system (4), (5) is dissipative and has a compact global attractor.*

## B. Equilibria

On the attractor structure, one can say more for the particular case (1), (2). Numerical simulations for this system show that all trajectories tend to equilibria. To understand this fact, let us recall the fundamental concept of cooperative systems<sup>16,17</sup>. The condition which determines a cooperative system<sup>16,17</sup> does not hold for (1), (2) but if we change variables to  $y_i = -x_i$ , then in the new variables in this system become cooperative. This fact implies that all local attractors are stable equilibria. The stable rest points  $(\bar{x}, \bar{v})$  of systems (1) and (2) can be found as follows. Let us set, for simplicity, that

$$\gamma_{ij} = \gamma_i \delta_{ij}, \quad \gamma_i > 0. \quad (13)$$

Setting  $dx_i/dt = 0$  in (1), we obtain  $\bar{x}_i = \gamma_i^{-1}(r_i - \rho_i(\bar{v}))_+$ , where  $f_+$  denotes  $\max\{f, 0\}$ . This gives the following nonlinear equation for  $\bar{v}$ :

$$D(S - \bar{v}) = \sum_{i=1}^N c_i \gamma_i^{-1} (r_i - \rho_i(\bar{v}))_+ \rho_i(\bar{v}). \quad (14)$$

This equation has an asymptotic solution for large turnovers  $D \gg 1$ . We obtain  $\bar{v} = S + O(D^{-1})$  and

$$\bar{x}_i = \gamma_i^{-1}(r_i - \rho_i(S))_+ + O(D^{-1}). \quad (15)$$

## III. EXTENDED TIME DEPENDENT PLANKTON MODEL

We extend system (4) and (5) to describe two important effects. The first effect is species extinctions. In reality abundances  $x_i$  are discrete numbers, therefore, if the abundance becomes too small, the corresponding species must become extinct. To describe this effect mathematically, we introduce a parameter  $\delta > 0$  and suppose that if the  $i$ -th species abundance  $x_i(t)$  becomes less than  $\delta$ , i.e.,  $x_i(t_0) = \delta$  and  $\frac{dx_i(t_0)}{dt} < 0$  for some  $i$  and  $t_0 > 0$ , then the corresponding species should be excluded from systems (4) and (5). We then set formally that  $x_i(t) \equiv 0$  for all  $t > t_0$ .

Note that after this modification the model stays mathematically well posed. In fact, let us introduce a function  $N_e(t)$ , which is the number of surviving species at time  $t$ , i.e. the number of indices  $i$  such that  $x_i(t) > \delta$ . It is clear that  $N_e(t)$  is a piecewise constant non-increasing function. Let  $t_0 < t_1 < \dots < t_m < \dots$  be the points of discontinuity of this function. Within the intervals  $[t_k, t_{k+1}]$  the Cauchy problem for systems (4) and (5) is well posed therefore the Cauchy problem is well posed for the modified systems (4) and (5) with extinctions. There are two possible situations. If  $\lim_{t \rightarrow +\infty} N_e(t) = N_\infty = 0$ , then all the species vanish. If  $N_\infty > 0$ , then on some infinite semiaxis  $(t_m, +\infty)$  the modified system is equivalent to the standard model, which has a compact global attractor. Therefore, in this case the modified model also has a compact global attractor. The time  $T_s$  when at least one species with  $x_j(t) > X_{ext}$  exists is called the survival time.

The second effect is a result of climate (environmental) influence on the dynamics of the modified systems (4) and (5) and species extinctions. To introduce dependence on the climate state (for example, on the average environmental temperature  $T$ ) we can assume that the resource depends on  $T$  and that  $T$  is a periodic function of time. We also include stochastic effects. For example, we can suppose that

$$S = S_0 + S_1 \sin(\omega t) + \varepsilon \eta(t) \quad (16)$$

where  $S_0, S_1 > 0$  are parameters,  $\omega$  is a frequency,  $\eta$  is standard white noise and  $\varepsilon$  is the noise amplitude. This means that the temperature changes periodically in time. The parameter  $S_0$  is a mean nutrient supply (resource), whereas the parameter  $S_1$  describes the intensity of periodic forcing.

To simulate chaotic time forcing we set

$$S = S_0 + S_1 \theta(t) + \varepsilon \eta(t) \quad (17)$$

where the function  $\theta$  can be obtained by chaotic trajectories of the Lorenz system, a rough model of atmospheric dynamics given by

$$\begin{aligned} dx/dt &= \tau^{-1}(\alpha(y - x)), \\ dy/dt &= \tau^{-1}(x(\rho - z) - y), \\ dz/dt &= \tau^{-1}(xy - \beta z), \end{aligned} \quad (18)$$

where  $\alpha, \beta, \rho$  are parameters and  $\tau > 0$  is a parameter that controls the speed of the trajectories. This system shows

chaotic behaviour for  $\alpha = 10, \beta = 8/3$  and  $\rho = 28$ . We construct  $\theta$  as follows. The third component  $z$  in (18) describes the time evolution of temperature. We set  $\theta(t) = (z(t) - \bar{z})/\mu_z$ , where  $\mu_z = \max(|z(t)|)$  on a large interval  $[0, T]$  and  $\bar{z}$  is the average of  $T^{-1} \int_0^T z(t) dt$  on this interval.

The time extended model reduces to the time independent model with constant  $S$  in the two opposite cases: (a)  $\omega \gg 1$  and (b)  $\omega \ll 1$ . Assume  $S = S(t)$  is defined by (16). In case (a), we can apply the averaging principle to (1), (2) and replace  $S(t)$  by  $S_0$  in (2). This averaging also works for  $S(t)$  defined by (17). The number  $N_e(t)$  of coexisting species tends to a constant for large  $t$ . This asymptotic approach is confirmed by numerical results in a large diapason of parameter values (see the next section).

In case (b) we introduce a slow time  $\bar{t} = \omega t$  and use the quasistationary approximation. Then we obtain that the equilibria  $\bar{x}(\bar{t}), \bar{v}(\bar{t})$  are functions of slow time. The number  $N_e$  of coexisting species is also a function of  $\bar{t}$ . Note that  $N_e$  is a measure of biodiversity.

#### IV. NUMERICAL RESULTS

We consider the Cauchy problem for the system given by (1) and (2) on a time interval  $[0, T]$ , where the initial data are given by

$$x_i(0) = X_i > 0 \quad (19)$$

and  $T$  is a positive number. We assume that  $N \gg 1$  (the case of a large ecosystem) and  $X_i > 0$  is distributed randomly according to a lognormal law with parameters  $a, \sigma$ . The corresponding distribution density is given by

$$f(x) = \frac{1}{x\sigma\sqrt{2\pi}} \exp \left[ \frac{-(\ln x - a)^2}{2\sigma^2} \right] \quad (20)$$

We assume that the coefficients  $a_i$  are random numbers obtained from the normal distribution  $\mathbf{N}(\bar{a}, \sigma_a)$ . Similarly  $K_i$  are distributed by  $\mathbf{N}(\bar{K}, \sigma_K)$ ,  $r_i$  are distributed by  $\mathbf{N}(\bar{r}, \sigma_r)$  etc. The share coefficients  $c_i$  are taken as random numbers uniformly distributed on  $[0, 1/N]$ . The other parameters are as follows: the turnover coefficient  $D \in [3, 20]$  and  $\omega \in [2, 8]$ , the species number  $N = 20$ , the time  $T = 10$ ,  $\delta = 0.1, X_0 = 1, V_0 = 10$  and  $\varepsilon \in [0, 10]$ .

In the numerical simulations, in order to simplify the problem, we assume that the concurrence is absent (condition (13) holds).

The following results are obtained. The number of coexisting species  $N_e(t)$  is shown on Fig. 1.

In some cases the strongly time oscillating supply  $S(t)$  defined by (16) can increase biodiversity,  $N_e(T)$  at  $S_1 = 0.8S_0$  is greater than  $N_e(T)$  at  $S_1 = 0$ , see Fig. 2. In case 1, we calculate the probability that the periodic oscillations of the nutrient resource will increase biodiversity. Also, we define the probability (case 2) that the periodic oscillations of the nutrient resource will decrease biodiversity. We note this plot (Fig. 2) is obtained by the Euler method with the time step 0.001 for

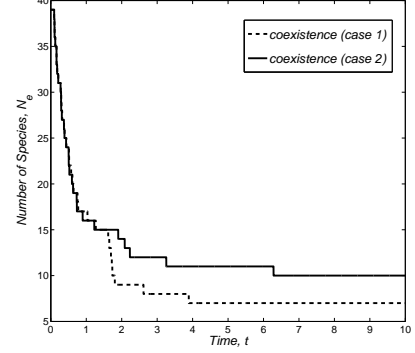


FIG. 1: This graph shows the number of coexisting species  $N_e(t)$  in the two cases. In case 1, the number of species  $N_e(T)$  coexists in a system depending on  $t$  when the nutrient supply  $S$  is a constant,  $S_0 = 200$  and  $S_1 = 0$ . In the case 2, the number of species  $N_e(T)$  coexists in a system with time varying resource,  $S_0 = 200, S_1 = 180$ .

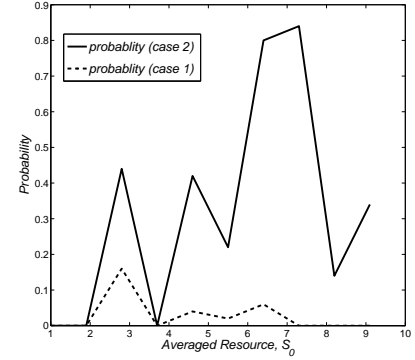


FIG. 2: This graph shows that in some rare cases the time oscillating supply  $S(t)$  can increase biodiversity. Here,  $S_1 = 0.8S_0$  for time depending model and  $S_1 = 0$  for time independent one. In case 1, the probability that the  $N_e(T)$  for the time dependent model is larger than  $N_e(T)$  for the time independent model with  $S_1 = 0$ . In case 2, the probability that the  $N_e(T)$  for the time dependent model is larger than  $N_e(T)$  for the model with  $S_1 = 0$ .

the following parameter values:  $N = 20, \bar{a} = 10, \sigma_a = 2, \bar{r} = 1, \sigma_r = 1, D = 3, T = 10, \bar{K} = 5, \sigma_K = 1$ . When the value of  $\varepsilon$  is large ( $\varepsilon = 10$ ) the noise is large. To compute the probabilities,  $M = 50$  solutions to the Cauchy problems were obtained with random data. The procedure was the same for both the time dependent and time independent models.

Fig. 3 displays the number of coexisting species on the averaged resource  $S_0$  vs time as presented in (16). Case 1 is the situation when the environment does not influence the system. In case 2  $N_e$  is always above that of case 1, this implies that the time oscillating resource diminishes biodiversity.

Fig. 4 shows the dependence of the number  $N_e$  on the speed parameter  $\tau$  when the resource  $S(t)$  evolves chaotically ac-

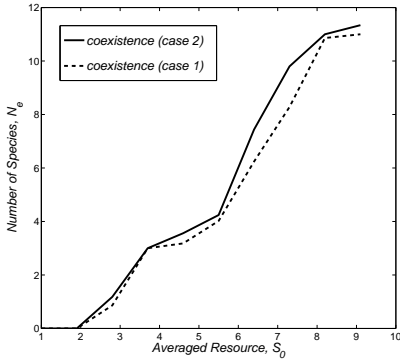


FIG. 3: This graph shows the dependence of the number of coexisting species on the averaged resource  $S_0$  in the case of (16). Case 1 corresponds to the record, where  $S_1 = 0$ . Case 2 corresponds to  $S_1 = 0.8S_0$ .

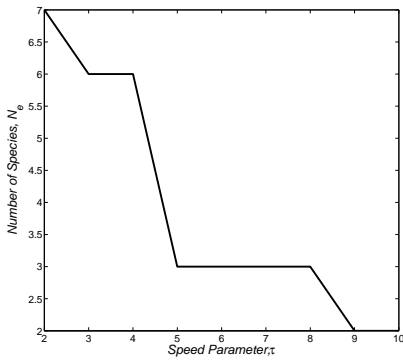


FIG. 4: This graph shows the dependence of the number  $N_e$  of coexisting species on the parameter  $\tau$  in the case of chaotic supply dynamics defined by (18). The time interval  $T = 80$ ,  $S_0 = 5$  and  $S_1 = 4$ .

cording to (18). We observe that the biodiversity is a decreasing function of the speed parameter. This decrease depends on the averaged supply level  $S_0$ , for larger  $S_0$  the effect is weaker.

Finally, the numerical and analytical results are as follows. For large values of  $S_0$  and  $\omega \in (3, 8)$ , when the period of time oscillations is much less, the system defined by (1), (2) shows formidable stability even for  $S_1$  close to  $S_0$ . The periodic and chaotic oscillations always decrease biodiversity, but the effect on coexisting species is small: the numbers  $N_e(T)$  remain close or they coincide. To obtain diminishing biodiversity, it is necessary to take  $S_1 = 0.95S_0$  which corresponds to the case of very strong oscillation. In seldom situations, the counter-intuitive effect of biodiversity increasing under oscillations is possible. It may happen when the averaged resource  $S_0$  is not large (see Fig.2). Note that this effect can be explained. In fact, the time oscillations and increasing supply can conserve some species which were close to extinction.

## V. CONCLUSION AND DISCUSSION

In this paper, a resource model for phytoplankton species is developed, which generalizes the well known model<sup>12</sup> and takes into account species self-regulation, extinctions, and time dependence of resources. Such conceptual models describe a simple and easily understandable mechanism for resource competition. For the case of fixed parameters, a general assertion on attractor existence for this model is proved. The sufficient condition of the attractor existence is that species self-regulation is stronger than the species competition. For the case of a single resource the large time behaviour of solutions can be described since then the system is cooperative. We find that all local attractors are stable steady points. These points can be found from a simple nonlinear equation for the equilibrium resource level. For large supply turnovers we find an asymptotic solutions of this equation.

In the case of time dependent resource oscillations two regimes are found which can be investigated analytically. The first regime describes fast oscillations. Then one can proceed by averaging the resource over time. The second regime arises when the resources change slowly, here we use the quasistationary approximation.

The numerical results show that when the averaged supply level is large enough, sufficiently fast resource time oscillations do not affect essential biodiversity, i.e., the number of coexisting species. This result is valid both for chaotic and periodic oscillations. The effect of oscillations becomes observable when the averaged resource value is sufficiently small. Then, typically, the oscillations (both chaotic and periodic) diminish biodiversity, however, in some cases oscillations with a noise component can increase biodiversity.

These results can be interesting for the biodiversity problem, where new ideas have been proposed recently (see <sup>18</sup> and also references therein). Some ecologists emphasized the roles of competition and environmental interactions in ecological system structure (niche theory). This niche model considers ecological selection as a driving force of ecosystem evolution. In contrast, so-called neutral models assume an equivalency between species and the role of stochasticity. In <sup>18</sup> it is shown that a transition is possible between two models, niche and neutral. The model <sup>18</sup> involves three terms: a term describing a species immigration into communities from a large regional species pool, a term that limits a species population to its carrying capacity and a stochastic force. Our model also includes different terms. It involves self-limitation terms and the resource term, which increases species populations but is much more sophisticated than the immigration term. Moreover, we consider noisy periodic and chaotic resource oscillations instead of purely stochastic forcing<sup>18</sup>. Instead of immigration, we consider an inverse process, namely, species extinctions. Our results lead to the conclusion that a chaotically varying environment only affects an ecosystem when the averaged resource level is not large enough. Then the resource rate decrease can lead to a sharp biodiversity decline.

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